*EXTRAIT DE MAMMALIA* TOME 24 N° 3 Septembre 1960

# STRUCTURE AND FUNCTION OF THE PHARYNGEAL POUCHES OF THE WALRUS (*ODOBENUS ROSMARUS* L.)

by

Francis H. FAY

*Arctic Health Research Center, U. S. Public Health Service, Anchorage, Alaska*

**Etude de la morphologie et du rôle des poches pharyngiennes d'*Odobenus rosmarus*. L'auteur énumère les différents tissus constitutifs des poches et leur origine, et montre qu'elles jouent peut-être un rôle dans la modification du poids spécifique de l'animal, ou servent de caisses de résonance, mais qu'elles n'ont aucun rôle dans la digestion.**

The physical characteristics of the pinniped family Odobenidae, of which the walrus is the only living representative, have been reviewed by Murie (1871) and Allen (1880) and, more recently, by Scheffer (1958). One character, apparently unique in these animals but not mentioned in the reviews, is the extreme elasticity of the pharynx, the lateral walls of which are expandable as a pair of large pouches or diverticula. Some northern aborigines, for whom walrus constitute an important source of food and structural materials, have traditionally made use of the pouches as drumheads and containers for storing food, and as a result of their experience and knowledge of pouch structure, these people have developed several theories regarding the function of the pouches and their importance to the walrus. There seems to be no published information on these interesting features other than a few remarks made by Pedersen (1930), Nikulin (1941), Vibe (1950), and Brooks (1954) ; therefore, it is the purpose of this paper to describe the structure of the pouches on the basis of several dissections and to review the evidence regarding their function.

## METHODS

The cervical region of two adult males, two adult females, two juvenile males, and two calves were examined preliminarily to determine the location and extent of the pouches. These animals

had been killed by Eskimo at Gambell, St. Lawrence Island, Alaska, in the process of the normal hunting activities, and each was completely butchered immediately after it was secured. Examination of these animals was necessarily done hastily and consisted of gross exploratory dissection of the neck, followed by digital probing of the interior of the pharynx and pouches. Three additional adult males, collected on Round Island, Bristol Bay, Alaska, were dissected in greater detail. From one of these the entire pharynx, from the tongue and soft palate to the oesophagus and trachea, was preserved in 10 per cent formalin for further study in the laboratory. The pharyngeal musculature of a third adult female was dissected in the field, and some information on location and size of the pouches in another was obtained from partial dissection of a decomposed carcass stranded on the south coast of St. Lawrence Island. Finally, details of the cervical musculature were determined from dissection of a calf which died in captivity at Gambell and was donated by the New York Zoological Society. Anatomy references used were Murie (*op. cit.*), Gray (1948), and Sisson and Grossman (1938). The anatomical terminology employed has been adapted from these.

Observations of the pouches in use were made mostly at Round Island during a four day period in late June, 1958. Notes concerning function also have been obtained in interviews with the St. Lawrence Islanders and from personal observation at various times in that locality. Dr. Carleton Ray, New York Zoological Society, made available information regarding a captive juvenile walrus, and James W. Brooks, Alaska Department of Fish and Game, Karl W. Kenyon, U. S. Fish and Wildlife Service, Seattle, and Vernon K. Slwooko, resident of Gambell, assisted in the field. The study was aided by a contract between the Office of Naval Research of the United States Navy and the Arctic Institute of North America.

## Location and Size of the Pouches

The pouches were stated by Pedersen, Nikulin, and Vibe to be evaginations of the oesophagus, whereas Brooks observed more precisely that they originate from the lateral walls of the pharynx. In three males examined in the present study, the mouths or ostia

of the pouches were situated posterior to the glottis and involved a small portion of the anterior end of the oesophagus (Fig. 1). In two others the ostia were lateral to the glottis, as Brooks reported. Each pouch was continuous with its respective *sinus piriformis*, the lateral recess of the pharynx.

Pouches were present in all of the adult males and in one of the four adult females examined. The pharynges of the other three mature females and of the juvenile males were extremely pliable but no special dilatations were evident, and the calves had even less modification for expansion. A captive male in the New York Aquarium showed no outward indication of pouch development at three years of age (C. Ray, personal communication).

From the ostia, the pouches extend dorsally and posteriorly, primarily between the axial and appendicular muscles of the neck. In most cases they extend no farther posteriad than the anterior border of the scapula, but in two of the animals examined there were large caudal extensions, nearly to the posterior edge of the thoracic cavity. These caudal extensions appeared to be covered by the latissimus dorsi, but field conditions did not permit adequate investigation of this relationship, nor that of their connection with the cervical portion of the pouches. Small postero-ventral extensions to the level of the first rib were also present in two specimens.

Unilateral expansion of the pouches was observed in several of the live animals at Round Island. In one of the specimens examined there, one pouch had a capacity of approximately 25 liters while the capacity of the other was less than one liter. With maximum development, each may have a capacity of more than 50 liters, according to Nikulin (p. 29), who evidently determined this by filling the pouches with a measured volume of water.

## Structure and Action

The pouches are composed of normal pharyngeal tissues, unmodified except in their enormous potential for elasticity. When inflated, they are rather thin-walled bladders with a reticulum of small bundles of muscles fibers radiating over the surface (Fig. 1). Blood vessels are few and sparsely distributed. In the preserved specimen, nine tissue layers were separable in gross dissection of each pouch,

the first layer being the visceral fascia and the ninth the mucosa and submucosa. Each of the seven intermediate layers was an aponeurosis-like continuation of several of the pharyngeal constrictors and the muscle layers of the oesophagus, as follows :

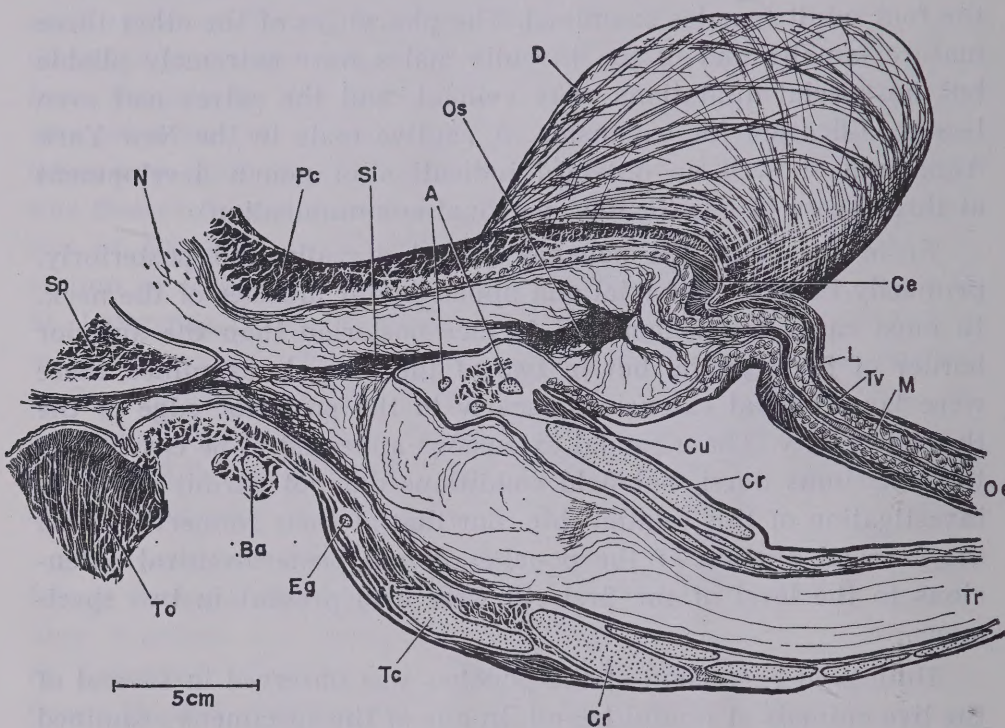


Fig. 1. — Pharynx of a male Pacific walrus in sagittal section, with a small, slightly inflated diverticulum on the right side. Moderate distortion due to fixing in 10 per cent formalin.

*A,* arytenoid cartilage ; *Ba,* basihyal ; *Ce,* m. ceratopharyngeus ; *Cr,* cricoid cartilage ; *Cu,* cuneiform cartilage ; *D,* diverticulum ; *Eg,* epiglottis cartilage ; *L,* m. longitudinalis ; *M,* mucus glands ; *N,* nasopharynx ; *Oe,* œsophagus ; *Os,* ostium diverticuli ; *Pc,* pharyngeal constrictors ; *Si,* sinus piriformis ; *Sp,* soft palate ; *Tc,* thyroid cartilage ; *To,* tongue ; *Tr,* trachea ; *Tv,* m. transversus.

*Cricopharyngeus.* — The second and third tissue layers of the pouches are derived from this muscle, which arises as two heads, one from the ventral half of the cricoid arch and the inferior cornu of the thyroid cartilage, and the other from the dorsal half of the cricoid arch. Both insert on the dorsal median raphé of the pharynx, where their fibers blend. Near the insertion, several fascicles

are continuous with the longitudinal layer of the oesophagus (Fig. 2, *a*).

*Thyropharyngeus.* — The fourth layer is from the thyropharyngeus, the largest and most conspicuous muscle of the pharynx. It originates as two major fascicles from the oblique line and lateral surface of the thyroid cartilage and inserts dorsally on the median raphé. At the insertion about half of the posterior fascicle is overlain by the cricopharyngeus, with which its fibers blend.

*Chondropharyngeus.* — This muscle does not contribute any tissues to the pouches, but it borders on the ostia and is closely allied to the next muscle, the ceratopharyngeus, with which its fibers are mixed at their common origin. Both arise from the posterior surface of the epihyal and ceratohyal bones and in some cases from the basihyal and ventral end of the thyrohyal. The chondropharyngeus proceeds dorsally and anteriorly, inserting on the median raphé and blending at the posterior edge with the anterior fascicle of the thyropharyngeus.

*Ceratopharyngeus.* — From its origin, this muscle radiates dorsally and posteriorly, inserting on the raphé and blending with the transverse muscle layer of the oesophagus (Fig. 1 and 2, *b*). Over the surface of the pouches, it was divisible into two distinct layers in the preserved specimen, but no bifurcation was evident in a fresh specimen dissected in the field.

*Pterygopharyngeus.* — Partly covered by the ceratopharyngeus is the pterygopharyngeus, which extends posteriorly along the sides of the pharynx, dividing into two fascicles at the level of the thyroid cornu of the hyoid. The ventral fascicle immediately terminates as a thick tendon which inserts on the posperior tip of the thyrohyal and continues postero-ventral to the muscular process of the arytenoid and to the anterior border of the thyroid cartilage (Fig. 2, *b*). The dorsal fascicle radiates over the lateral wall of the pharynx, inserting in part on the raphé and mixing posteriorly with scattered clumps of glandular tissue which represent the anterior extension of the oesophageal mucus glands. This constitutes the seventh tissue layer of the pouches.

*Stylopharyngeus.* — The eighth tissue layer, apparently continuous with the stylopharyngeus, is seen posterior to the hyoid as a thin layer of slender fasciculi radiating along the lateral wall of the pharynx. It blends posteriorly with the pterygopharyngeus and the scattered bundles of glandular tissue (Fig. 2, *b*).

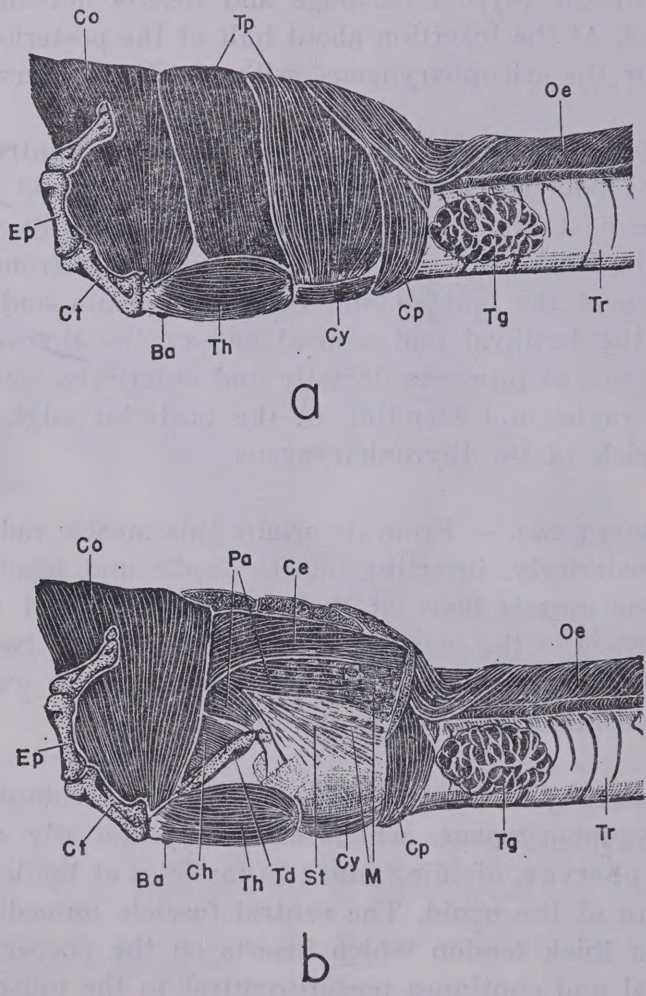


Fig. 2. — Lateral view of the pharynx of a female Pacific walrus with no pouches developed, showing : (a) the pharyngeal constrictors, and (b) the inner, longitudinal muscles.

*Ba,* basihyal ; *Ce,* m. ceratopharyngeus ; *Ch,* m. ceratohyoideus ; *Co,* m. chondropharyngeus ; *Cp,* m. cricopharyngeus ; *Ct,* ceratohyal ; *Cy,* m. cricothyroideus ; *Ep,* epihyal ; *M,* mucus glands ; *Oe,* œsophagus ; *Pa,* m. pterygopharyngeus ; *St,* m. stylopharyngeus ; *Td,* Thyrohyal ; *Tg,* thyroid gland ; *Th,* m. thyrohyoideus ; *Tp,* m. thyropharyngeus ; *Tr,* trachea.

It is clear from the structure of the pouches that they cannot be expanded except by force from within. Under normal conditions this force is exerted by air exhaled from the lungs while the oesophageal muscles and the anterior pharyngeal constrictors are tensed. Once the pouches are inflated, the longitudinal muscles and portions of the constrictors prevent the air from escaping, evidently by a combination of constriction and compression of the ostia. The need for exceptional muscle control is apparent, and the massive development of the pharyngeal and oesophageal musculature seems to be correlated with the great magnitude of opposing forces exerted upon the pouches by the cervical muscles and sheer weight of the overlying skin and blubber. Deflation is accomplished merely by relaxing the pharyngeal constrictors.

From the condition of pouches in the animals examined it was apparent that contraction, following deflation, is gradual. Several days or weeks may pass before the pharyngeal walls return to their former, non-expanded position.

### Function

In describing a carnivorous walrus which he examined in East Greenland, Pedersen (p. 390) noted that the « ... whole stomach and crop-like widening of the oesophagus... were filled with seal blubber », implying that the diverticula are part of the alimentary system. Later, Vibe (p. 33) briefly discussed the suggestion by Dr. Poul Hansen that the walrus' « crop » might be a place where mussels are held « in order to force them open ». Vibe personally doubted this, since the Eskimo of Northwest Greenland had never reported finding any food in the pouches. The theory that the pouches function as alimentary organs has never been supported by any evidence other than that of Pedersen's specimen, which, I believe, was the result of an accident. I have successfully inflated the pouches of a dead walrus by means of a hand-operated air pump inserted into the cardiac end of the oesophagus, and I suppose that the seal blubber which Pedersen found could have been expelled from the full stomach into the pouches as the animal died.

In the combined experience and tradition of walrus hunting Eskimo interviewed in Greenland, Canada, and Alaska by Vibe, A. W. Mansfield (personal communication), and Brooks, there was no knowledge of food or anything other than air having been found

in the pouches. Similarly, the walrus hunters of St. Lawrence Island, some of whom have travelled widely on the Siberian coast, and all being closely related or acquainted with walrus hunters in Northeast Siberia, have no record of personal observation or traditional stories regarding food in the pouches. It is unanimously agreed by these people that the pouches never contain anything but air and that they are used principally for buoyancy, especially when the animals sleep in the water. This function was described briefly by Nikulin (pp. 29-30), Vibe (p. 46), and Brooks (p. 25), each on the basis of independent observations or interviews with reliable observers.

In my own experience at least eight walrus have been seen sleeping in the water, and each had its pouches inflated. The positions assumed when sleeping in this manner ranged from nearly horizontal to vertical. Of the most horizontally oriented animals, part of the back, shoulders, and neck was exposed above water, and the head was raised periodically from its submerged position in order to breath. Of the most vertically oriented animal, an adult male, only the head and about one-third of the inflated neck were out of water, with the rostrum pointed skyward and the tusks held horizontally. This animal was killed instantaneously as it slept, whereupon the pouches deflated and the carcass sank immediately, demonstrating the high specific gravity of the animal and the importance of the inflated pouches in maintaining his position at the surface. The specific gravity of females is often low enough that air retained in the lungs is sufficient to keep them afloat, which may account for their tendency to inflate their pouches less frequently than the males.

The pouches are used in regulating specific gravity during some activities other than sleeping. They were inflated in many of the animals seen loafing or swimming about Round Island, and several times at St. Lawrence Island I have seen bulls inflate their pouches after having been wounded by rifle bullets. Obviously, greater equilibrium with the surrounding water reduces the effort required in swimming and especially in rising to the surface for air. This is clearly an advantage to the wounded animal and a convenience, at least, to normal individuals.

Two other possible functions which have been suggested but not investigated are the storage of a reserve air supply and the production of sound. The St. Lawrence Islanders report that

during the winter, when walrus surface for air in the small leads and holes in the ice, the animals generally inflate their pouches with the last breath exhaled before diving. Some of these people believe that air carried in this manner serves as a reserve oxygen supply which can be re-inhaled for protracted submergence. Specific information on the $O_2$ capacity and the respiratory function in walrus is needed to determine this, but I suspect that the volume of $O_2$ in the exhaled air is insignificant in contrast to the $O_2$ capacity of the total haemoglobin and myoglobin of the animal. Assuming that the $O_2$ capacity of walrus is at least as great per volume of blood and muscle as that of some seals (see Scholander, 1940), I estimate that a 3000 pound male would have a capacity in excess of 100 liters of $O_2$, whereas the air in its pouches could contain no more than 10 liters, or less than 1/10 of the total oxygen supply.

Regarding production of sound, the St. Lawrence Islanders and the people of Barrow (Brooks, p. 25) believe that the pouches are used in some way to produce a repetitive, bell-like tone which is made while the animals are submerged. This sound resembles the toll of distant church bells but with a deep resonance and variable pitch typical of aquatic transmission. While at Round Island I heard this several times from small groups of animals which were loafing and diving in the shallow water near shore. In each of these groups there was one or more with its pouches inflated, but because of the obscure nature of the sound, which seems to come from all sides, it was not possible to determine its exact source or its connection, if any, with the use of the pouches.

From the aspect of phylogeny, it would be of some interest to determine the comparative anatomy of the pharynx in the living genera of pinnipeds. I am aware of no record of pharyngeal diverticula in any but *Odobenus,* though I expect that some of the larger otariid and phocid seals may have developed this specialization for pelagic living. Since most of the anatomical descriptions of pinnipeds have been based upon dissections of young animals, it is conceivable that important structures of this type, which may not develop until physical maturity, have been overlooked.

*
* *

F. H. Fay. — Structure et fonction des poches pharyngiennes du Morse (*Odobenus rosmarus*).

*Résumé*

Dans cet article, l'auteur étudie la structure et la fonction des poches pharyngiennes du Morse (*Odobenus rosmarus*). Les poches pharyngiennes, présentes chez tous les mâles adultes examinés et chez une femelle adulte sur quatre, ne sont que très peu marquées chez les jeunes adultes et presque inexistantes chez les jeunes. Elles ont leur origine dans les parois latérales du pharynx et si, vers l'arrière, elles ne dépassent pas généralement les épaules, il arrive qu'elles s'étendent jusqu'à l'arrière de la cage thoracique. Elles ne sont pas toujours développées également, l'une pouvant avoir un volume de 25 litres et l'autre d'un seul litre. Nikulin (1941) donne plus de 50 litres comme maximum pour chaque poche, dans le cas de développement symétrique.

Ces poches sont constituées par du tissu pharyngial normal, non modifié sauf en ce qui concerne une extrême élasticité. Elles sont peu vascularisées. Les parois sont constituées par 9 couches de tissus : la première couche étant le faisceau viscéral, les 2e et 3e proviennent du cricopharyngien ; la 4e du thyropharyngien, les 5e et 6e du cératopharyngien, la 7e du ptérygopharyngien, la 8e du stylopharyngien, la 9e étant la muqueuse.

Les poches n'ont rien à voir avec le tube digestif, au point de vue fonction, et servent à changer le poids spécifique de l'animal par exemple pour lui permettre de dormir en mer.

Il est possible que ces poches servent aussi de réservoir d'air pour la respiration, mais l'auteur ne le pense pas du fait que la quantité d'oxygène contenu dans les poches est négligeable (le dixième) par rapport à la quantité d'oxygène retenue par le sang et les muscles.

Il est possible que les poches aient un rôle dans le son répété, à résonnance de cloche, que les animaux émettent quand ils sont immergés, mais l'auteur ne peut l'affirmer.

Il serait intéressant de rechercher pour les autres Pinnipèdes s'il existe chez les adultes de semblables organes.

*
* *

## Literature cited


Allen J. A. (1880). — History of North American pinnipeds. *U. S. Geol. Geog. Surv. Terr., Misc. Publ.*, 12, 785 pp.

Brooks J. W. (1954). — A contribution to the life history and ecology of the Pacific walrus. *Alaska Coop. Wildl. Research Unit, Spec. Rep.*, 1, 103 pp.

Gray H. (1948). — Anatomy of the human body. 25th Ed., edited by C. M. Goss. Philadelphia, *Lea and Febiger*, 1.478 pp.

Murie J. (1871). — Researches upon the anatomy of the pinnipedia. Part I : On the walrus (*Trichechus rosmarus*, Linn.). *Proc. Zool. Soc. London*, 7 (4) : 411-464.

Nikulin P. G. (1941). — Chukotski morzh. *Izvestiia TNIRO*, Vladivostok, 20 : 21-59.

Pedersen A. (1930). — Fortgesetzte Beiträge zur Kenntnis der Säugetier — und Vogelfauna der Ostküste Grönlands. *Medd. om Grönl.*, 77 (5) : 341-507.

Scheffer V. B. (1958). — Seals, sea lions, and walruses. London, *Oxford Univ. Press.*, 179 pp.

Scholander P. F. (1940). — Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrådets Skr.*, Nr. 22, 131 pp.

Sisson S., and J. D. Grossman (1938). — The anatomy of the domestic animals. 3rd Ed., Philadelphia, *W. B. Saunders*, 972 pp.

Vibe C. (1950). — The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on ice conditions in 1939-41. *Medd. om Grönl.*, 150 (6) : 1-115.